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Deviations of treeline Norway spruce radial growth from summer temperatures in East-Central Europe

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ABSTRACT

While some cold regions show evidence of recent decoupling of tree-ring growth from observed temperature rise, i.e. restricted growth increase, similar evidence from other regions is missing. Increasing or diminishing regional coherency in tree growth has also been observed over recent decades. The temporal and spatial extent of the abovementioned processes are poorly known and their drivers are not well understood. Pollution and changing climate have often been discussed as a cause of divergent or convergent growth patterns and deviations of growth from driving climatic variable. We compiled climatic records and robust tree-ring chronologies of treeline *Picea abies* covering 1920–2010 for four regions in East-Central Europe (Czech Republic, Poland, Slovakia, 50°N, 15–20°E) which experienced differing acid pollution loads. The divergence of these chronologies from Jun-Jul temperatures was compared with temperature and pollution trends. We found a period of low intra-regional growth coherency in the 1950s reflecting warmer, less temperature-limiting conditions and land use change. Highly coherent growth in the 1930s, 1970s and 1980s was related to the strong environmental growth-limiting signals of short growing seasons and high acid pollution loads. In all regions, we identified periods with higher (1940–1960s) and lower (1970–1980s) growth than expected based on temperature. In the high-frequency domain, the effect of pollution on growth departure from temperature was limited and detectable exclusively in regions that were most impacted by pollution. In the low-frequency domain, the departures of growth from temperature were caused by combined effects of the changing seasonal window of tree growth sensitivity to climate and pollution load. These results highlight the need to recognize non-stationary noise in the relationship between temperature and tree growth.

1. Introduction

Mountain forests are crucial carbon sinks (Kurz et al., 2007), making it vital to understand their growth dynamics. Production of stem biomass in mountain forests is primarily affected by competition, disturbance and environmental constraints (Pretzsch et al., 2014). The latter includes climatic variables, among them temperature, which has been showing an almost uniformly increasing trend over recent decades (IPCC, 2014). In the temperate zone of Europe, growth responses of mountain forests to increasing temperature have been predominantly positive in terms of radial growth (Leal et al., 2007; Hartl-Meier et al., 2014), with some exceptions from the lower part of the montane forest zone (Ponocná et al., 2016). The strongest positive responses have been reported from treelines (Rolland et al., 1998; Oberhuber, 2004; Treml et al., 2015a). However, growth divergence (i.e. decoupling of growth curves from temperature trends) has been observed across many temperate and boreal forests (Wilson et al., 2007; D'Arrigo et al., 2008), even for temperature-limited trees close to their upper or northern limits (D'Arrigo et al., 2004; Wilmking et al., 2005; Galván et al., 2015). Since there is also evidence that trees in some cold regions do not display signatures of growth divergence (e.g. treelines in the Alps, Büntgen et al., 2008), the degree to which trees are decoupled from

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climatic forcing, and the spatial and temporal extent of this phenomenon, remains unknown.

In temperature-limited environments, a weakening of the link between radial growth and temperature has been observed in several regions of Canada and Alaska (D'Arrigo et al., 2004; Wilmking et al., 2004), Siberia (Jacoby et al., 2000), Northern Europe (Schneider et al., 2014 for maximum wood density), the Pyrenees (Galván et al., 2015) and Central Europe (Wilson and Elling, 2004). The observed divergence has been attributed to, for instance, the intervention of other climatic limiting factors such as drought in Canadian and Alaskan treeline areas (Barber et al., 2000; Lloyd and Fastie, 2002). In montane forests of Central Europe, divergence has been ascribed to the effect of sulfur and nitrogen air pollution (Wilson and Elling, 2004, Godek et al., 2009, Rydval and Wilson, 2012). It has been suggested that divergence in other areas, particularly boreal forests (D'Arrigo et al., 2008; Stine and Huybers, 2014), has been due to the effect of "dimming" (i.e. decrease in incident solar radiation due to increasing concentration of aerosols in the atmosphere). However, Büntgen et al. (2008) argued that no divergence appears in high-elevation tree-ring chronologies from the Alps, with most treeline chronologies tracking both high and low-frequency temperature variations well.

In our region of interest – Central Europe – growth divergence has been observed not only in mountain but also in lowland tree-ring chronologies. This includes oak chronologies since the 1980s (Dobrovolný et al., 2016; Prokop et al., 2016) and also some silver fir chronologies (Wilson and Elling, 2004; Büntgen et al., 2011). Although pollution has been suggested as a probable cause for fir, the sudden decrease in climate sensitivity of oak remains unresolved.

In contrast to observed growth divergence from climatic trends, another general pattern related to changing climatic conditions has recently emerged – increasing convergence of growth patterns within regions (Shestakova et al., 2016). Under increasing environmental stress (e.g. increasing drought severity and/or frequency) tree growth coherency increases as well (Shestakova et al., 2016; Tumajer and Treml, 2017). Based on this pattern, assuming that growth of treeline trees is limited by temperature (Körner, 2012), their growth coherency should decrease if they are subjected to warming, which may be accompanied by a decrease in strength of the temperature signal in treeline tree-ring chronologies. On the other hand, pollution, as a stressor, could become a driver of convergence in growth patterns.

In this study, we hypothesized that the possible decoupling of tree growth from temperature forcing will be proportional to the pollution load or the degree of warming. We also hypothesized that decoupling will be more obvious in low-frequency variability than in the high-frequency components of time series. This is because the influence of previously negligible or absent variables affecting growth (i.e. pollution, extension of the growing season) are thought to gradually shift the prevailing climate response (D'Arrigo et al., 2008). To test these hypotheses, we built representative tree-ring chronologies, similar in terms of age and site representation, for four treeline areas with a differing air pollution load.

2. Material and methods

2.1. Geographic setting

The focal area for our study is the mountainous area of East-Central Europe (i.e. the region situated at 50° N latitude and between 15° and 20° E longitude, Fig. 1). The study region comprises crystalline areas of the Krkonoše Mts. (KRK), the Jeseníky Mts. (JES), both belonging to the Bohemian Massif, and flysch, crystalline and limestone massifs of the Carpathians (Babia Góra Mts. - BAB, Nízké Tatry Mts. - NT) with elevations ranging from 1491 to 2056 m a.s.l. Norway spruce (*Picea abies* L. Karst.) dominates montane forests up to the timberline. Prostrate dwarf pine (*Pinus mugo*) is also widespread in the treeline ecotone except at JES. The climate is cold (mean treeline growing season temperature is 6.7 °C, (Kaöpar and Treml, 2016) and humid, with annual precipitation totals ranging from 1200 mm in JES to 1500 and 1800 mm on the summits of BAB and KRK, respectively (Kwiatkowski, 1982; Migała, 2005). Soils of the montane forests are mostly podzols, dystric cambisols, and rankers (Tomášek, 1995; Granec and Šurina, 1999).

The lower limit of the alpine treeline ecotone (i.e. so-called timberline) increases toward the east from 1240 m a.s.l. in KRK to 1320 m a.s.l. in JES, ca. 1370 m a.s.l. in BAB and 1410 m a.s.l. in NT, with maximum timberline positions about 100 m higher than the above-mentioned mean values (Treml and Migoń 2015, Czajka et al. 2015a). Since the second half of the 20th century, treeline ecotones have been gradually advancing upwards as a consequence of land-use change and warming (Czajka et al., 2015b; Treml et al., 2016). During the 1970s and 1980s, forests in the study area were affected by acid pollution resulting in growth suppression and increased mortality (Sander et al., 1995; Rydval and Wilson, 2012). The major pollution sources were situated in the boundary region of Germany, Poland and the Czech Republic, which was reflected in a pronounced gradient in reaction to pollution from the western (strongest response) to the eastern part of the study area.

2.2. Sampling and sample processing

Increment cores from co-dominant or dominant *P. abies* growing at timberline were collected in KRK, JES, BAB, NT between 2010 and 2012 (Table 1). Each region was represented by two to three sites located on different slope aspects. Mean tree height was about 10 m. All sites were without visible recent human intervention (e.g., no evidence of recent logging or grazing). Two cores per tree were taken at breast height (approx. 1.3 m above the ground) perpendicular to the slope. Cores were prepared using standard dendrochronological methods (Stokes and Smiley, 1996). Core samples were mounted on wooden supports and sanded, and tree-ring width (TRW) was measured to the nearest 0.01 mm with a TimeTable measuring stage (Vienna Institute for Archaeological Science). The minimum sample depth for tree-ring chronologies was 40 trees. Tree-ring chronologies were assembled based on similar age structures among the sites, because differences in age structure might produce differences in growth trends (Carrer and Urbinati, 2004; Nehrbass-Ahles et al., 2014). In most regions, the originally extensive sample sets (~60–70 trees) were thus reduced by removing certain age cohorts of trees.

Each TRW growth curve contains an age trend, which should be removed through tree-ring standardization (Cook and Pederson, 2011) prior to the extraction of environmental information. We performed standardization procedures that retain medium to low-frequency variability in growth (i.e. variability on the order of several decades). Since standardization approaches differ in their sensitivity to the age structure of samples (Helama et al., 2004) and in their ability to mitigate the so-called end effect (Melvin and Briffa, 2008), we employed two different standardization procedures. First, we performed individual-based detrending using splines with a 66% variability cut-off at 90 years (i.e. approximate mean series length at each site) (Treml et al., 2012) and signal-free standard chronologies ("SPLINE") were created (Melvin and Briffa, 2008). Such chronologies preserve medium-frequency growth variability and are free of end effects (Melvin and Briffa, 2008). These chronologies were created using CRUST software (Melvin and Briffa, 2014). Second, basal area increment chronologies (BAI) were constructed by converting tree-ring widths to ring areas (Biondi and Qeadan, 2008). BAI transformation was performed in R (package 'dplR') using the BAIin function. Although pith offset was not accounted for, we only used tree-ring cores that reached the pith or those with a very limited estimated number of missing rings to the pith (three missing rings at maximum). BAI chronologies are good at preserving low- to medium-frequency growth variability (Biondi and Qeadan, 2008; Hartl-Meier et al., 2014), however, they fail to track

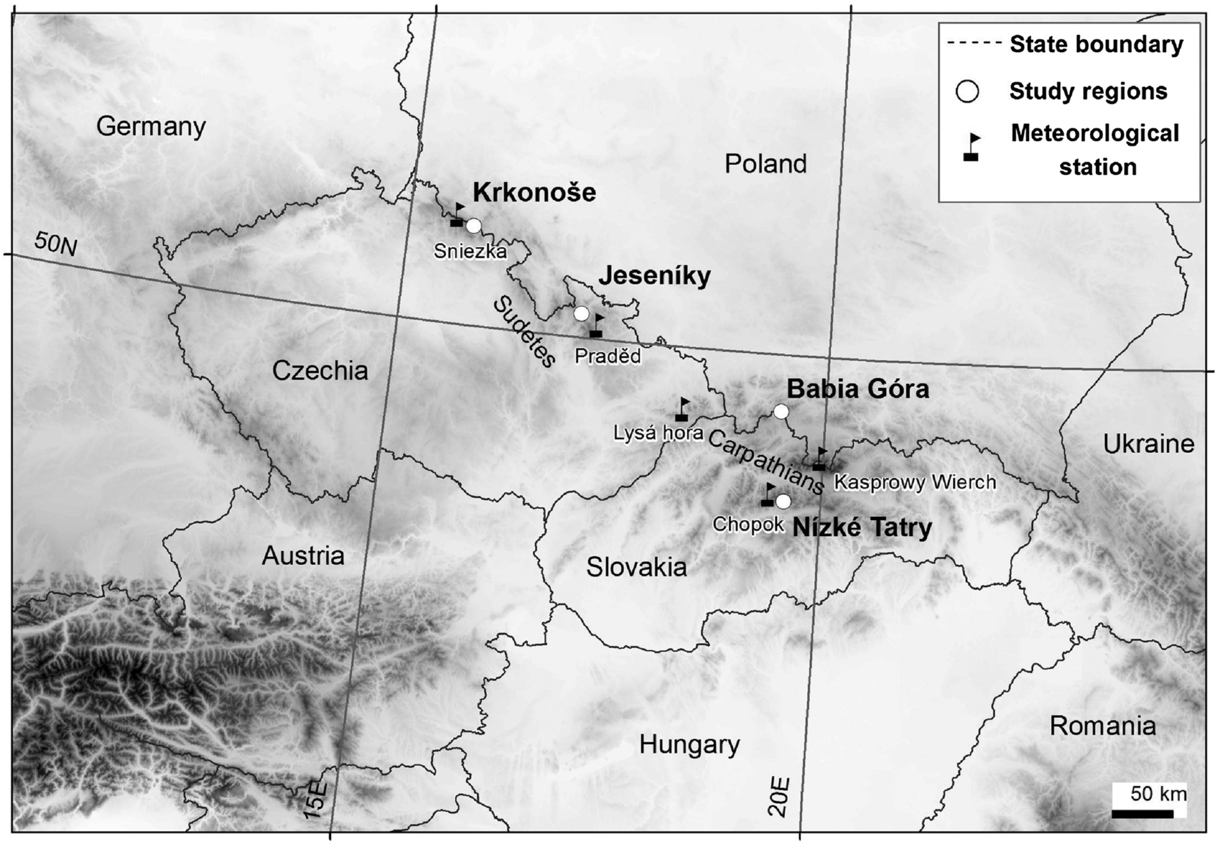

Fig. 1. Locations of study areas: Krkonoše Mts., Jeseníky Mts., Babia Góra Mts. and Nízké Tatry Mts.

environmental signals in periods represented by juvenile growth phases of sampled trees (Sullivan et al., 2016).

2.3. Temperature data

For dendroclimatological procedures, climate data with monthly resolution are usually satisfactory (Cook and Kairiukstis, 1990). Treeline tree-ring chronologies in the study area are especially sensitive to June and July temperatures (Ponocná et al., 2016; S1, Suppl.); therefore, the time series of average values of June and July temperatures were used in our analyses. However, we faced two challenges. First, we wanted to obtain temperature series that were as long as possible and, second, we aimed to work with climate series truly representative of high-elevation treeline climates (Weber et al., 1997). Whenever possible, we used station data (WMO 12510 Sniezka – KRK, 1613 m a.s.l., 1901–2010, Migała et al., 2016). In other cases, we used both long-gridded temperature series from the CRU TS data set (Harris et al., 2014) and available shorter (1961–2010) high-elevation station data from Lysá hora (1322 m a.s.l., WMO 11787), Kasprowy Wierch (WMO 12650, 1989 m a.s.l., these stations were representative of BAB) and Chopok (WMO 11916, 2007 m a.s.l., representative of NT). The Sniezka temperature record was used also for the JES region due to very good agreement ($r = 0.98$) with local station data from Praded – 1492 m a.s.l. (1948–1998). Furthermore, BAB CRU Jun–Jul series diverged from averaged nearest high-elevation station data (Lysá hora, Kasprowy Wierch) since the mid-1980s (Fig. 3). Therefore, a composite time series of Jun–Jul temperature departures from 1961 to 1990 means was developed using CRU data covering 1901–1961 and mean values from Lysá hora and Kasprowy Wierch representing the period 1961–2010 (Fig. 3).

2.4. Growth-climate coherency

The basic parameters of tree-ring chronologies (TRW, mean sensitivity, first-order autocorrelation) were compared across regions using ANOVA. Coherence in growth trends among individual TRW series within each region was inspected using inter-series correlations (Rbar, Cook and Kairiukstis, 1990) using a moving window with a length of 21 years and a 1-year step. For both types of tree-ring chronologies (SPLINE, BAI) and for temperature series, trend breakpoints (i.e., the points where regression coefficients change) were determined using the R package strucchange (Zeileis et al., 2015). For this analysis, the minimum segment length was set to 20 years.

We computed the correlations of original (unfiltered) TRW and Jun-Jul temperature series and for high and low-frequency time series. High and low-frequency series were obtained by filtering the original series with high- or low-pass Gaussian filters with a 20-yr window. In addition, moving correlations over 21-yr intervals with a 1-yr step were

Table 1
Basic site and chronology characteristics.

Region	Number of sites	Site aspect	Site elevation (m a.s.l.)	Number of trees in chronology	Mean segment length (± SD)	Chronology start/end
Krkonoše	3	SW,E	1300	49	122 ± 29	1830/2010
Jeseníky	3	SW,E	1350	49	108 ± 24	1836/2010
Babia Góra	2	S,W	1450	40	126 ± 29	1841/2012
Nízké Tatry	2	S,W	1450	43	119 ± 35	1823/2012

calculated.

Finally, TRW chronologies and Jun–Jul temperatures were scaled to unit variance and zero mean, and differences (residuals) between TRW and temperature were computed for unfiltered, high and low-frequency series (Büntgen et al., 2008). Buffers representing the 5th and 95th percentiles of normal distributions were derived to highlight extreme values.

We attempted to explain the residual variability by environmental factors other than Jun–Jul temperature (i.e. the modelled sulfur and nitrogen loads). Correlations of TRW residuals (unfiltered, high- and low-frequency time series) with sulfur and nitrogen deposition were therefore also computed. Estimated historical sulfur and nitrogen regional depositions were calculated according to the method of Oulehle et al. (2016). This method is based on the tightly coherent relationship between measured precipitation, SO_4, NO_3 and NH_4 concentrations from 32 monitoring sites, and Czech and Slovak national emission rates of SO_2, NO_x and NH_3 for the period 1994–2012. The skillful performance of this method in estimating historical emissions suggests that its long-term reconstruction and prediction of sulfur and nitrogen deposition is robust. We calculated sulfur and nitrogen deposition for the period 1950–2010 for each region (KRK, JES, BAB, NT).

Besides pollution, the potential instability in the relationship between Jun-Jul temperature and TRW might also be caused by a changing seasonal window of growth sensitivity to temperature. That is why the 21-yr moving correlations with monthly temperature variables were computed for the months with an observed influence on tree growth (April to August of the ring formation year, (Ponocná et al., 2016); S1, Suppl.). Furthermore, the growing season length was computed for each timberline area according to Paulsen and Körner (2014) – growing season was defined as the period with daily mean temperature higher than 0.9 °C and no snow pack. Temperature and precipitation from mountain stations was used and scaled to timberline elevation using the local environmental temperature gradients. For computational details see Kaöpar and Treml (2016). Growing seasons were subsequently classified as short (less than 15th percentile), average (15th–85th percentile) and long (more than 85th percentile). The effect of growing season length (factor levels – short, average, long) on TRW residuals and on correlations between TRW and monthly temperatures was tested by ANOVA with post-hoc tests.

3. Results

3.1. Growth coherency and tree-ring width chronologies

Mean values of TRW, mean sensitivity and TRW autocorrelation decrease from west to east (S2, Suppl.). TRW series coherency as indicated by Rbar (Fig. 2) showed widespread depression between the early 1940s and the beginning of the 1960s and in the 1920s (absent in KRK). Peak coherency was achieved in the 1970s (all regions) and the most recent decades (1990 onwards, KRK, JES). High growth coherency was also observed in the 1930s in all regions with the exception of KRK. Before 1960, mean Rbar was similar among regions, with values between 0.3 and 0.4. Between 1960 and 1970, Rbar increased to 0.6 with the exception of NT, where Rbar continued to be relatively stable.

All SPLINE and BAI chronologies are characterized by two pronounced growth peaks (Fig. 3). The first occurs in the 1940s–1960s, the second in the 2000s. Whereas in the BAB, NT and KRK SPLINE chronologies the first peak is rounded and culminates at the turn of the 1950s and 1960s, the JES and KRK BAI chronologies culminate in the late 1940s and then decrease. The prominent growth suppression in the 1970s and 1980s was common to all chronologies, with a minimum in the early 1980s. The two culmination points of the SPLINE TRW chronologies achieved in the 1940s and 2000s have approximately the same values. BAI chronologies displayed maximum growth in the 2000s (JES, BAB, NT) with the exception of the KRK BAI chronology, which exhibited a maximum growth point in the 1940s. Compared to TRW

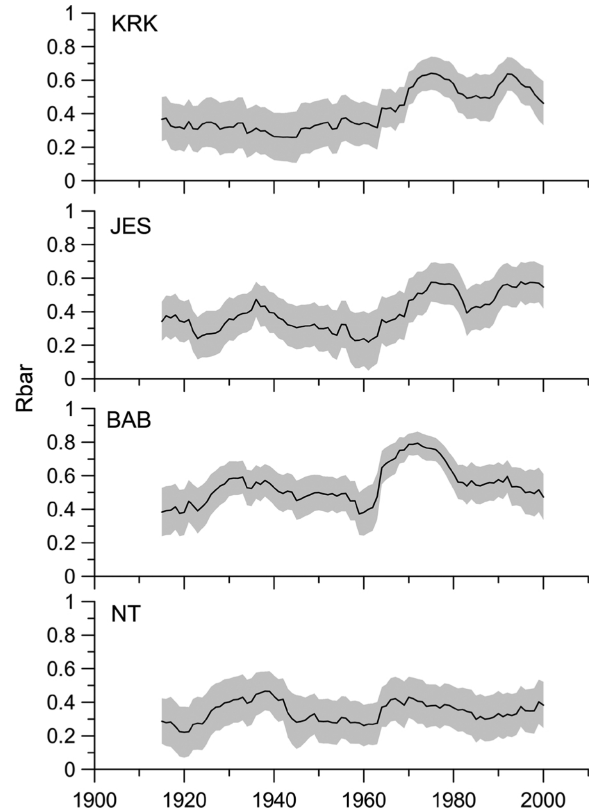

Fig. 2. Coherency of standardized tree-ring width series as indicated by moving inter-series correlations (Rbar). Correlations were computed for 21-yr windows with a 1-yr step. Lines and buffers denote means and standard deviations, respectively. Abbreviations: KRK - Krkonoše Mts., JES - Jeseníky Mts., BAB - Babia Góra Mts., NT - Nízké Tatry Mts.

series, the depressions in Jun–Jul temperature in the 1970s and early 1980s, as well as in the 1920s are relatively minor. The same is true for the positive anomaly in the 1950s. Jun–Jul temperatures attained their maximum values in the 2000s in all regions.

Trend breakpoints of SPLINE and BAI tree-ring chronologies are dated to 1943 (KRK, JES), 1930 (BAB) and 1934 (NT) meaning that increasing growth was replaced by a decreasing growth trend (Fig. 3). In 1979 (KRK, JES) and 1973 (BH, NT), the negative trend in TRW indices turned positive again. The only trend breakpoint in Jun-Jul temperature occurred in 1972 or 1973 in all regions.

3.2. Coherency of tree-ring width chronologies with Jun–Jul temperature

For unfiltered time series, SPLINE chronologies were, on the whole, slightly less correlated with Jun–Jul temperature (r = 0.51–0.53 and r = 0.45 for NT) than BAI chronologies (r = 0.53–0.59), with the exception of KRK (r = 0.43) (Appendix S1, Suppl.). In the case of the high-frequency time series, the correlations with temperature were approximately the same as for the unfiltered time series (r = 0.51–0.61), with only NT showing lower correlation (r = 0.43–0.46). For time series showing low-frequency variability, there was good agreement between both SPLINE and BAI chronologies and temperature for JES. KRK had substantially better coherence between SPLINE and temperature than between BAI and temperature, whereas the opposite was true for BAB and NT (Appendix S1, Suppl.).

The 21-yr moving correlations of unfiltered TRW and Jun–Jul temperature between 1920 and 2010 (Fig. 4A) are statistically significant over the entire study period with the exception of NT around 1960 (i.e. 1950–1970 window). Highest correlations were achieved around 1930 (1920–1940 window), in the 1940s and in late 1980s (only JES and BAB). Relatively low correlations were found for the

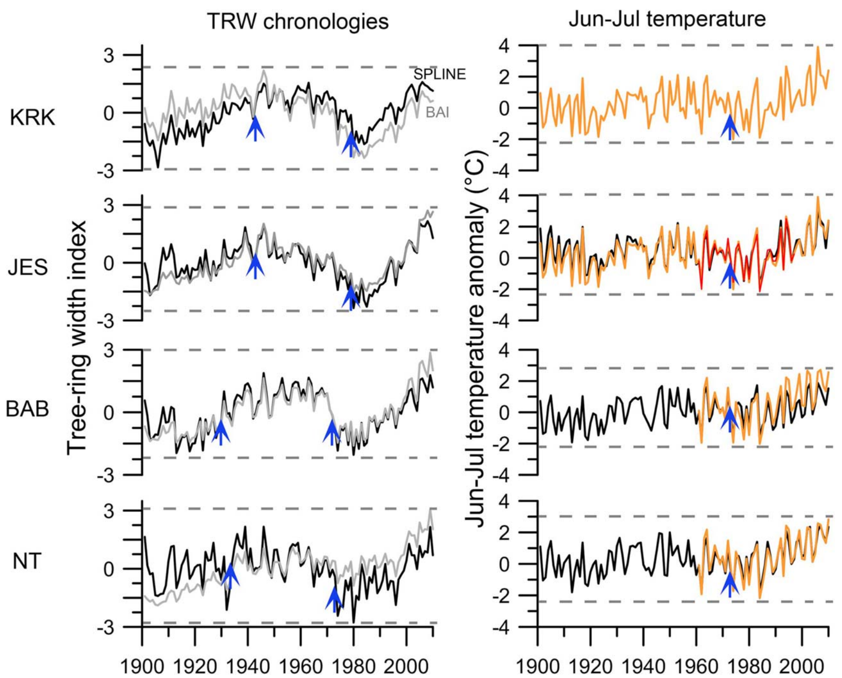

Fig. 3. Individually-detrended SPLINE and basal area increment (BAI) tree-ring chronologies and Jun–Jul temperatures in the four study regions (KRK, JES, BAB, NT). CRU temperatures (gridded data set) are in black, station temperatures (used in analysis) are in orange or in red (reference station time series from Praděd /JES/). Blue arrows denote trend breakpoints; dashed lines indicate minimum and maximum values. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

period between approximately 1955 and 1980. For high-frequency time series (Fig. 4B), the correlation decreased slightly from the 1950s onwards with a steeper drop in the 1990s and 2000s. The moving correlations of the low-frequency chronologies (Fig. 4C) showed a pronounced decrease in the 1940s and 1950s for all regions, and a second depression in the early 1980s with a substantial drop for KRK and JES. A less pronounced correlation decrease was observed for BAB and relatively small or almost no (BAI chronology) oscillation for NT.

TRW residuals (i.e. chronology departures from Jun–Jul temperature series, Fig. 5, left) showed a cluster of positive values in the 1940s and 1950s, and negative values between the 1970s and 1990s (KRK, JES, BAB). This pattern is less obvious in NT, where a cluster of positive anomalies in the 1940s and 1950s was interrupted around 1950, and the BAI chronology did not display prevailing negative departures in the 1970s or 1980s. For high-frequency time series (Fig. 5, middle), positive and negative departures of TRW from Jun-Jul temperatures are regularly distributed with no obvious clusters. In KRK, however, the two greatest negative anomalies are dated to 1982 and 1983. Low-pass filtered time series (Fig. 5, right) are characterized by high positive TRW residuals in the 1940s to 1960s (KRK, BAB, NT; 1940s–1950s in JES), greater negative anomalies in TRW than in Jun–Jul temperature in the 1970s–1990s, and recent positive TRW residuals (in the 2000s). Low-frequency trends vary between SPLINE and BAI chronologies in KRK and NT. In KRK, negative departures of TRW from temperature are rather limited for the SPLINE chronology in the 1970s and 1980s. In contrast, the BAI chronology shows continuous negative departures of

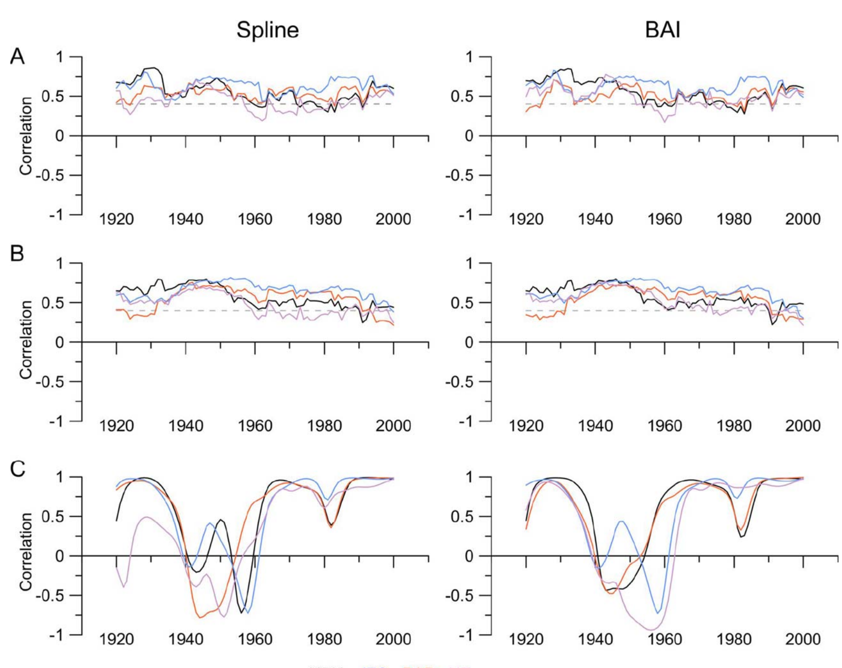

Fig. 4. Moving correlations between TRW chronologies and Jun–Jul temperature for unfiltered (A), high-pass (B) and low-pass (C) filtered chronologies. The dashed line denotes the significance threshold - p = 0.05 (not shown for highly autocorrelated low-frequency time series).

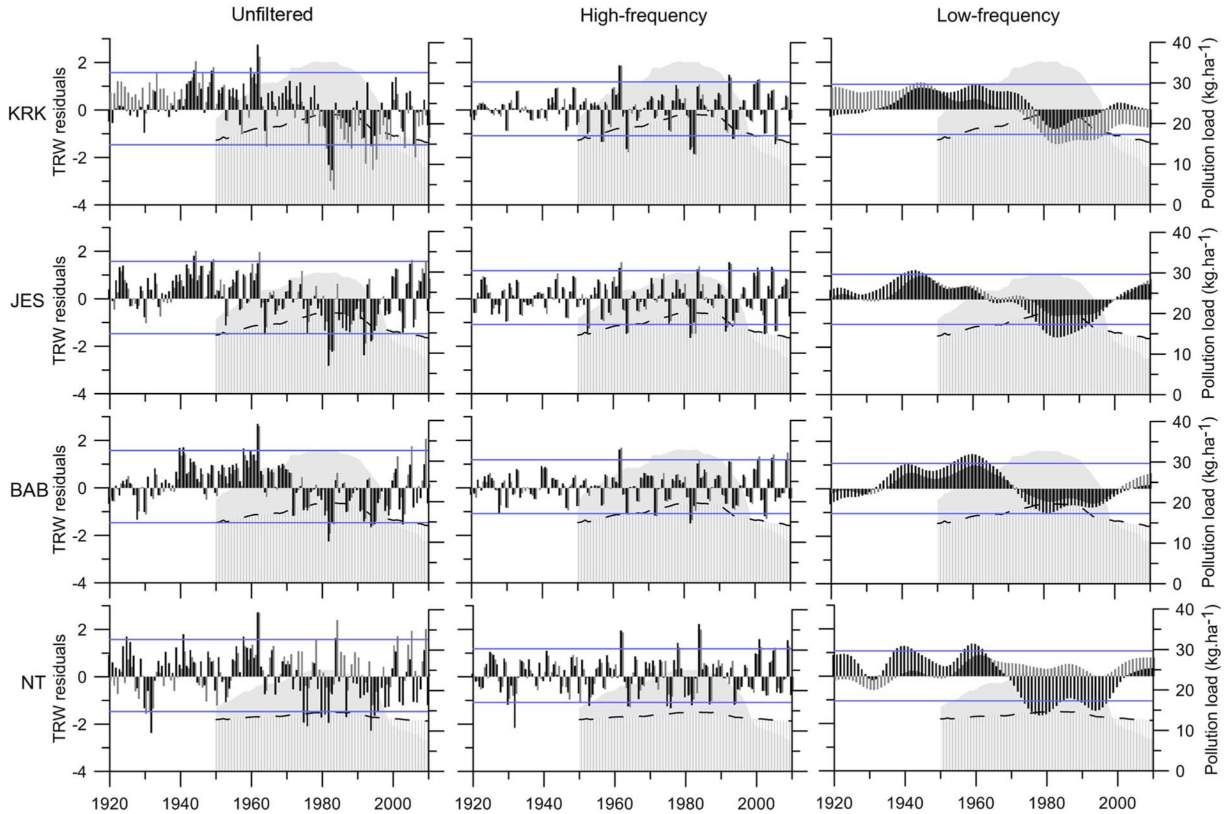

Fig. 5. Departures of tree-ring indices from Jun–Jul temperature for unfiltered, high-frequency and low-frequency time series together with sulfur deposition (gray area) and nitrogen deposition (dashed line and patterned area). Departures of SPLINE chronologies are in black and BAI chronologies in dark gray. Blue lines indicate the lower (5%) and upper (95%) bounds of the confidence limit. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

TRW from Jun-Jul temperatures from the 1970s to the present. In NT, the BAI chronology revealed a continuous slightly positive departure from temperature since the 1950s.

3.3. Factors affecting deviations of tree-ring width from Jun–Jul temperature

Correlations between unfiltered TRW residuals and sulfur and nitrogen deposition were highest and significant for JES and BAB (Fig. 6). KRK BAI residuals were also significantly correlated with nitrogen deposition. The remaining relationships were not statistically significant. In the low-frequency domain (Fig. 6), TRW residuals were significantly correlated with both nitrogen and sulfur deposition for JES chronologies. Nitrogen deposition was also significantly correlated with TRW residuals of NT-SPLINE and BAB-BAI chronologies.

To further explain clustering of TRW departures from Jun–Jul temperature in certain periods (i.e., trend divergence between Jun–Jul temperature and TRW), the seasonal window of tree growth and the moving correlations of high-pass filtered TRW and temperature variables were computed (Fig. 7A). Compared to average or short growing seasons, the long growing seasons were characterized by higher positive TRW residuals ($p < 0.05$, Fig. 7B) and significantly higher correlations with July and August temperatures (Fig. 7C). TRW residuals in short growing seasons did not differ from those in average growing seasons (Fig. 7B), however short growing seasons were characterized by low correlations of TRW with August and July temperatures (compared to average and long growing seasons, $p < 0.05$) and relatively high correlations with June temperatures (significantly higher than during long growing seasons, $p < 0.05$, Fig. 7C). The greatest negative TRW residuals in the 1970s and 1980s were coincident with a very short growing season in all areas except NT.

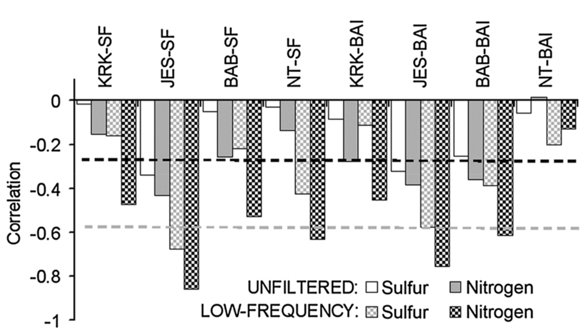

Fig. 6. Correlations of residuals (TRW – JJ; unfiltered, low-pass filtered time series) with modelled depositions of sulfur (S) and nitrogen (N) (1950–2010). Dashed lines indicate p = 0.05 with correction for low degrees of freedom of autocorrelated low-pass filtered time series (gray line).

4. Discussion

Our treeline tree ring chronologies capturing the period since the early 20th century showed varying tree growth coherency (Fig. 2) and variable strength of the relationship between tree growth and summer temperature (Fig. 5). Increases in growth coherency were observed in the 1930s (all regions except NT) and 1970s (all regions). The late 1930s contained periods with very short growing seasons. In addition, during the second half of the 1930s, all chronologies exhibited rapidly increasing correlations of TRW with Jun-Jul temperature indicating that coherent growth was driven by a common temperature factor. Intra-regional coherent growth patterns since the 1970s were probably initially a consequence of strong environmental drivers in the form of increasing acid pollution and cooling. In the latter part of the recent warming period (1990s to the present), growth coherency decreased again, however, it was still higher compared to the 1950s and 1960s,

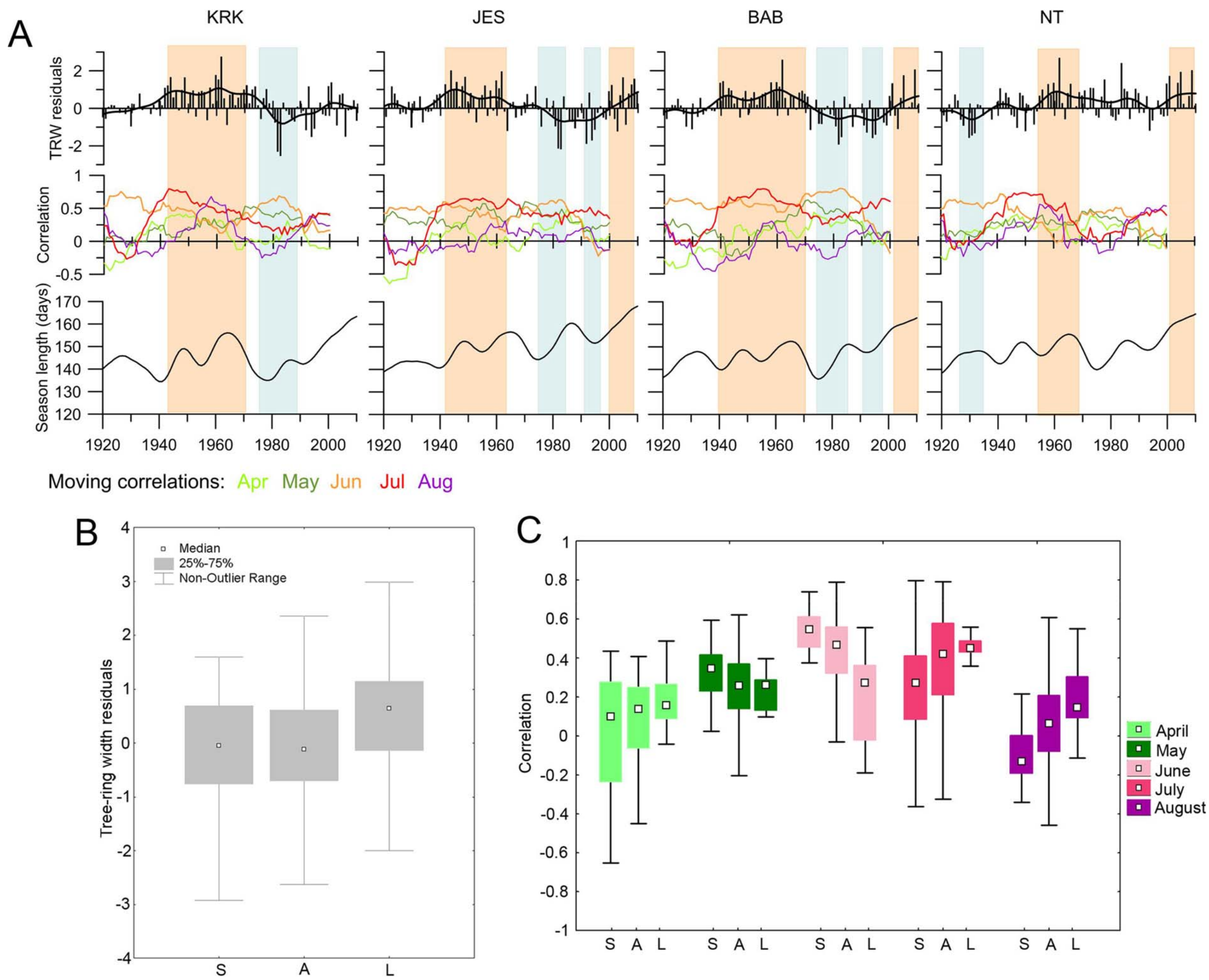

Fig. 7. (A) TRW residuals (unfiltered – bars, low-pass filtered – lines) together with moving correlations between TRW and monthly temperature variables and growing season length in each area (Krkonoše - KRK, Jeseniky - JES, Babia Góra – BAB and Nízké Tatry - NT). Red and blue stripes denote clustered positive (red) and negative (blue) residuals. (B) TRW residuals in short (S), average (A), and long (L) growing seasons. (C) Correlations between TRW and mean monthly temperature for short (S), average (A), and long (L) growing seasons. For each area, TRW residuals refer to the TRW chronology showing best agreement with Jun–Jul temperature (SPLINE for KRK, BAI for JES, BAB and NT). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

particularly in KRK and JES. In those regions, the recent increase in growth coherence might result from a uniform response of trees to newly released nutrients in soils due to enhanced decomposition of organic matter (Kolář et al., 2015). This process has been observed in locations previously affected by acidification, which is not necessarily true for areas with naturally less acidic soils such as BAB or NT.

In all areas, the growth coherency was lowest in the 1950s when shifts in growth-climate responses also occurred. The 1950s represent the second-warmest period captured in our chronologies, with correspondingly high growth rates. The limiting influence of temperature was probably lower in the warmer 1950s which led to more individualistic growth and thus lower growth coherency as indicated by lower Rbar. In addition, the period from the 1940s to the 1950s was characterized by complete (KRK, JES) or partial (BAB, NT) cessation of cattle grazing and hay-harvesting, leading to forest encroachment (Kozak, 2003; Treml et al., 2016). The localized (i.e. at the site or even the individual tree level) increase in competition or decrease from grazing pressure might then have underlain increasing variability in growth trends during the 1950s.

The analysis of departures of TRW from Jun–Jul temperature revealed their different patterns in high and low-frequency domains. In high-frequency variability, no clustering of residuals was observed, meaning that short-term fluctuations in temperature were reflected in TRW with more or less temporally stable noise and almost no detectable effect of pollution. In contrast, low-frequency time series exhibited systematically higher positive or negative departures in periods with longer (late 1940s to early 1960s, 2000s) or shorter (1970s and 1980s, 1920s in BAB) growing seasons, respectively. From the 1940s to the 1960s, high departures of TRW from Jun–Jul temperature were synchronous with shifts in growth-climate correlations during the period of long growing seasons. The most apparent change was the abrupt decrease of the correlation with June temperature and increase of the influence of July and August temperatures. We also observed temporary increases in TRW correlations with April or May temperatures.

We propose that the extension of the time-window of TRW sensitivity to temperature was probably responsible for the detected decrease in climate signal strength. Evidence from on-site measurements of growing season duration at the timberline in KRK (sampling period 2010–2012) supports this suggestion (Treml et al., 2015b). The initiation of radial growth occurred between the beginning of May and late May with the main phase of cell production occurring between May and July, but lasting until early August in the growing season with the highest cell production (Treml et al., 2015b). High cell production rates in growing seasons with an early beginning usually lead to a delay of the end of the cell enlargement phase (Rossi et al., 2013). The window with the greatest sensitivity of radial growth to climate (i.e. the period of cell division and cell enlargement, Kulmala et al., 2017) thus shifted considerably. The same could be anticipated for the period between the

late 1940s and 1960s. Clustering of growing seasons with prevailing early or late onset of radial growth therefore probably results in shifts in the growth-climate response. This is also apparent in the prevailingly strong responses of TRW to July temperature in long growing seasons and the predominant importance of June temperatures during short growing seasons (with cell division and enlargement constrained to a shorter period).

For unfiltered and low-pass filtered series, the highest negative departures of TRW from Jun–Jul temperatures occurred in the late 1970s and early 1980s. Lower than expected growth was probably a consequence of acid pollution together with short growing seasons and a corresponding decrease in correlation with July temperature (see above). In the 1990s and 2000s, TRW departures turned positive again, indicating the change in growth-climate response (this interval exhibited the longest growing season duration within the 1901–2010 study period). This positive trend could also represent the influence of additional stimulating factors (e.g. nutrient release – Kolář et al., 2015). However, positive departures in the 1990s and 2000s were still smaller than those in the 1950s. Our results therefore show that the recent growth increase has followed the temperature increase with relatively minor deviations.

The impact of acid pollution on the climate signal in treeline trees was clear for the unfiltered and low-pass filtered series. The correlations between TRW residuals and acid deposition were strongest in JES and BAB, and relatively weak in KRK, which is the area with the highest pollution load. This discrepancy might to some extent be explained by interference from acid deposition and instability in the growth-climate response driven by changing seasonality in KRK. The difference between the growing season length in the 1960s (peak) and 1970s and 1980s (minimum) in KRK was the greatest among all regions under study, indicating the most significant shift in the window of TRW sensitivity to temperature. Low correlations between TRW residuals and pollution load in KRK might also be attributed to a relatively weak reaction of TRW to decreasing pollution and increasing temperature in the 1990s and 2000s when the BAI chronology continued to display lower values than expected based on Jun–Jul temperatures. These negative residuals might reflect inertia in the response of tree growth to soil acidification, because the recovery of soils substantially lags behind the decrease in acid deposition (Hruška et al., 2002). Surprisingly, we also found a stronger response of TRW residuals to nitrogen than to sulfur deposition. However, both substances acidified the environment simultaneously and their effect was probably additive.

For Central Europe, Ponocná et al. (2016) showed that regional differences among treeline chronologies are substantially smaller than among chronologies representing montane forests, and that only in KRK was the effect of acid pollution clearly expressed across the entire elevation range of spruce distribution. As also demonstrated in our study, the high similarity of treeline chronologies suggests a strong, although non-stationary, climatic forcing of treeline tree growth, which partially masks the effect of pollution. Vacek and Lepš (1996) demonstrated that acid pollution affects dense stands more heavily than open ones, which could possibly explain the observed pattern of unambiguous pollution impact on (dense) montane forests (Rydval and Wilson, 2012; Kolář et al., 2015; Čada et al., 2016) and the less obvious, complex response of treeline stands.

Our study proposes possible causes of growth divergence from summer temperature of treeline *P. abies* in Central Europe. It seems that the acid pollution in the 1970s and 1980s was an important but not the only reason for varying divergence of TRW from summer temperature in the 20th and 21st centuries. We suggest that in further studies employing linear transfer functions between temperature and TRW (a typical approach to climate reconstruction, Fritts, 1976), the calibration period should be long enough to capture periods with positive and negative departures of TRW from the driving climatic variable. Otherwise, prevalence of positive or negative residuals in the calibration period might distort the resulting reconstructions. This might also apply to estimation of the effect of acid pollution on growth reduction based on calibration of TRW with temperature in periods not-affected by pollution (e.g., Rydval and Wilson, 2012). If the calibration window is too short, it might contain a prevailing period of naturally higher or lower than expected growth and thus distort the growth projection in the modelled period. We have also shown that two commonly employed approaches (individual spline detrending and BAI) sometimes differ in their representation of the amplitude and duration of extreme growth episodes. Therefore, any comparisons of TRW and climatic variables will benefit from providing uncertainty estimates that consider instabilities in growth-climate responses captured using various TRW standardization approaches (e.g., Büntgen et al., 2010; Treml et al., 2015a). In conclusion we propose that the list of factors causing temporarily limited reductions of tree growth response to temperature contains not only changes in stand openness (Rydval et al., 2016), drought (Wilmking et al., 2005), pollution (e.g. Wilson and Elling, 2004, this study), reduced inter-annual temperature variability (Schneider et al., 2014), but also shifts in climate signal in periods with prevailing long or short growing seasons.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.agrformet.2018.02.001.

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